

## Five new species of *Myrsidea* Waterston (Phthiraptera: Menoponidae) from saltators and grosbeaks (Passeriformes: Cardinalidae)

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### Abstract

Five new species of *Myrsidea* parasitic on members of the avian family Cardinalidae are described. They and their type hosts are *M. lightae* ex the Buff-throated Saltator, *Saltator maximus* (Statius Müller, 1776), *M. markhafneri* ex the Slate-colored Grosbeak, *S. grossus* (Linnaeus, 1766), *M. pittendrighi* ex the Streaked Saltator, *S. striatipectus* Lafresnaye, 1847, and *M. johnklickai* and *M. sychrai* ex the Blue-black Grosbeak, *Cyanocompsa cyanoides* (Lafresnaye, 1847). Results from sequences of a portion of the mitochondrial COI gene for several specimens of two of these species and other species of *Myrsidea* are presented.

**Key words:** chewing lice, mitochondria, COI gene, sequencing

### Introduction

Five new species of *Myrsidea* Waterston from avian hosts in the passerine family Cardinalidae (saltators and grosbeaks) as delimited by Dickinson (2003) are described and illustrated.

In the following descriptions, all measurements are in millimeters. Abbreviations are TW, temple width; HL, head length; PW, prothorax width; MW, metathorax width; AWIV, abdomen width at segment IV; ANW, female anus width; GL, male genitalia length; and TL, total length.

The holotypes of the new species are deposited as indicated following each description, either in the collection of the National Museum of Natural History, Smithsonian Institution, Washington, D.C. (USNM), or the collection of the Illinois Natural History Survey, Champaign, Illinois (INHS). Paratypes are distributed between these two collections.

Sequences of a portion of the mitochondrial COI gene were obtained for two of the species described herein. These were compared to sequences of other *Myrsidea* to evaluate the genetic distinctiveness of these species and their possible phylogenetic relationships.

### Genus *Myrsidea* Waterston

*Myrsidea* Waterston 1915: 12. Type species: *Myrsidea victrix* Waterston, 1915, by original designation.

A thorough characterization of the morphology of members of the genus *Myrsidea* may be found in Clay (1966). Additional features and illustrations, including a drawing of an entire louse and discussion of charac-

ters in common with typical species, may be found in some recent descriptions of new species of this genus (e.g., Price and Dalgleish 2007). For brevity, these points are not repeated in the species descriptions that follow.

***Myrsidea lightae* Price, Johnson, and Dalgleish, new species**  
(Figs. 1–4)

**Type host.** *Saltator maximus* (Statius Müller, 1776), the Buff-throated Saltator.

**Female.** Head with strongly developed hypopharyngeal sclerites; gula usually with 5 setae on each side, much less often only 4. Dorsovenital metathorax and abdomen as in Fig. 1. Metanotal posterior margin with 17–21 setae; metasternal plate with 6, less often 5 or 7, setae. Tergite I much enlarged with pronounced tapered medioposterior convexity, this resulting in compression of tergites II–VI. Each tergal setal row with distinct median gap. Tergal setae: I, 13–20; II, 17–22; III, 17–24; IV, 17–22; V, 15–23; VI, 16–21; VII, 14–20; VIII, 9–16. Postspiracular setae on III and V–VI <0.25 long, all on these segments distinctly shorter than the extremely long setae on II, IV, or VIII; those on VII intermediate in length between these shorter setae and the extremely long ones. Pleurites: I–III with relatively uniform short setae; IV–VII with fine longer setae toward midline; VIII with long seta flanked on each side by much shorter seta. Sternal setae: II, 5 in each aster, less often 4, 16–21 marginal between asters, 6–12 anterior; III, 32–35; IV, 42–52; V, 40–53; VI, 33–43; VII, 15–20; VIII–IX, 18–27. Anus with 34–40 ventral, 38–46 dorsal fringe setae. Dimensions: TW, 0.51–0.56; HL, 0.34–0.36; PW, 0.33–0.35; MW, 0.51–0.59; AWIV, 0.68–0.75; ANW, 0.24–0.28; TL, 1.67–1.82.

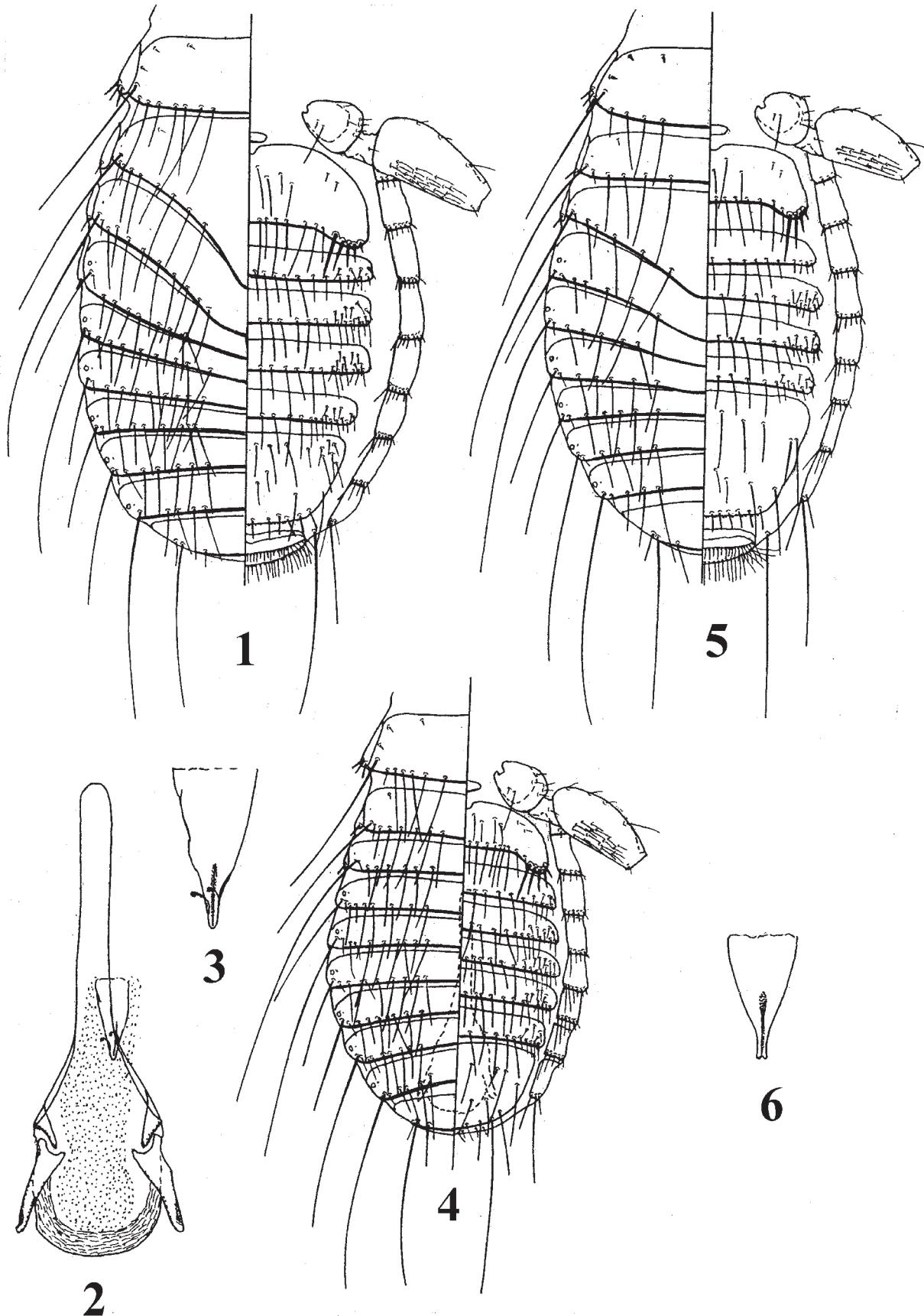
**Male.** Head, thorax, median gap in abdominal tergal setal rows, lengths of postspiracular setae, and chaetotaxy of abdominal pleurites as for female (Fig. 4), except for only 13–19 marginal metanotal setae. Tergal setae: I, 13–17; II, 16–21; III, 18–22; IV, 16–20; V, 17–22; VI, 16–20; VII, 15–20; VIII, 12–15. Sternal setae: II, 5 in each aster, less often 4, 15–19 marginal between asters, 9–14 anterior; III, 24–33; IV, 39–46; V, 39–47; VI, 36–41; VII, 18–31; VIII, 7–12. Genitalia as in Fig. 2; genital sac sclerite (Fig. 3) posteriorly tapered, with median dark line and each side with small slender subapical process. Dimensions: TW, 0.46–0.50; HL, 0.31–0.33; PW, 0.30–0.32; MW, 0.41–0.45; AWIV, 0.52–0.57; GL, 0.46–0.49; TL, 1.34–1.47.

**Type material.** Holotype female (to INHS), ex *S. maximus*, **PANAMA:** Serriana del Maje, 16 Feb. 2006, JMD 603, K.P. Johnson. Paratypes (to INHS), all from type host: 1 female, 1 male, same data as holotype; 3 females, 2 males, same except JMD 656; Paratypes (to USNM) **COSTA RICA:** 3 females, 3 males, Punta Cocles Hotel, 10 km E. Pto. Viejo, Limon, 24–25 Apr. 1992, R.L. Fisher 228, R.C. Dalgleish; 1 female, 1 male, La Selva Biological Station, Puerto Viejo, 11–14 June 1992, R.L. Fisher 399, R.C. Dalgleish; 1 male, Monte Anivo Lodge, 13 km N. Portero Grande, Punterenas, 17 May 1995, Fisher 2124, R.C. Dalgleish; **VENEZUELA:** 2 females, 1 male, 60 km E. Sta. Elena, Edo. Bolivar, Jan. 1987, R.C. Dalgleish.

**Other material.** Ex *S. striatipectus* Lafresnaye, 1847, **PANAMA:** 1 female, 2 males, Serriana del Maje, 16 Feb. 2006, JMD 687, K.P. Johnson; **COSTA RICA:** 5 females, 1 male, Las Cruces Biological Station, Cota Brus, 18–21 Apr. 1992, R.L. Fisher 80, R.C. Dalgleish.

**Remarks.** This species represents the first of three described here that have a median gap in the abdominal tergal rows. The female is easily separated from those of the other two by the much enlarged abdominal tergite I (Fig. 1 vs. Figs. 5 and 9) and the large number of setae on the abdominal tergites. The male may be distinguished by its quantitative abdominal tergal chaetotaxy and its large dimensions. In addition, both sexes have typically five setae in each sternite II aster, rarely four on one side, as opposed to the other two species always having four setae on both sides, rarely three on one side.

**Etymology.** This species is named in honor of Jessica Light, University of Florida, Gainesville, Florida, in recognition of her work on louse systematics and coevolution.



**FIGURES 1–6.** 1–4. *Myrsidea lightae*. 1. Female dorsoventral metathorax and abdomen. 2. Male genitalia. 3. Male genital sac sclerite. 4. Male dorsoventral metathorax and abdomen. 5–6. *M. johnklickai*. 5. Female dorsoventral metathorax and abdomen. 6. Male genital sac sclerite.

***Myrsidea johnklickai* Price, Johnson, and Dalgleish, new species**  
(Figs. 5–7)

**Type host.** *Cyanocompsa cyanoides* (Lafresnaye, 1847), the Blue-black Grosbeak.

**Female.** Head with strongly developed hypopharyngeal sclerites; gula usually with 4 setae on each side, less often only 3. Dorsoventral metathorax and abdomen as in Fig. 5. Metanotal posterior margin with 9–10 setae; metasternal plate with 6 setae. Tergite I of normal size, tergite II much enlarged with pronounced tapered medioposterior convexity, resulting in compression of tergites III–VI. Each tergal setal row with distinct median gap. Tergal setae: I, 11–15; II, 14–16; III, 12–18; IV, 13–16; V, 12–15; VI, 13–15; VII, 12–16; VIII, 10–14. Postspiracular setae on III and V–VI <0.25 long, all distinctly shorter than the extremely long setae on II, IV, VII, or VIII. Pleurites: I–III with relatively uniform short setae; IV–VII with fine longer setae toward midline; VIII with long seta flanked on each side by much shorter seta. Sternal setae: II, 4 in each aster, rarely 3, 13–16 marginal between asters, 10–14 anterior; III, 16–21; IV, 26–35; V, 30–36; VI, 24–30; VII, 10–14; VIII–IX, 20–26. Anus with 26–34 ventral, 27–36 dorsal fringe setae. Dimensions: TW, 0.45–0.47; HL, 0.31–0.34; PW, 0.28–0.31; MW, 0.41–0.45; AWIV, 0.55–0.63; ANW, 0.20–0.21; TL, 1.47–1.56.

**Male.** Head, thorax, median gap in abdominal tergal setal rows, lengths of postspiracular setae, and chaetotaxy of abdominal pleurites as for female (Fig. 7), except for only 8–9 marginal metanotal setae and rarely 5 setae on metasternal plate. Tergal setae: I, 10–12; II, 13–14; III, 12–15; IV, 13–14; V, 11–14; VI, 11–14; VII, 11–15; VIII, 8–10. Sternal setae: II, 4 in each aster, rarely 3, 11–15 marginal between asters, 9–14 anterior; III, 16–21; IV, 22–28; V, 25–31; VI, 22–26; VII, 10–15; VIII, 5–6. Genitalia as in Fig. 2; genital sac sclerite (Fig. 6) posteriorly tapered, with median dark line but lacking small slender subapical processes. Dimensions: TW, 0.42–0.43; HL, 0.29–0.31; PW, 0.26–0.29; MW, 0.35–0.40; AWIV, 0.46–0.48; GL, 0.40–0.45; TL, 1.24–1.33.

**Type material.** Holotype female (to INHS), ex *C. cyanoides*, **PANAMA:** Serriana del Maje, 15 Feb. 2006, JMD 591, K.P. Johnson. Paratypes, all from type host: 2 males, same data as holotype; 1 female, 2 males, same except JKO6-024; paratypes (to USNM) **COSTA RICA:** 5 females, 2 males, Las Cruces Biological Station, Cota Brus, 27 June 1993, R.L. Fisher 675, R.C. Dalgleish; 3 females, 1 male, La Selva Biological Station, 11–14 June 1992, R.L. Fisher 376, R.C. Dalgleish; **VENEZUELA:** 2 females, 3 males, 60 km E. Sta. Elena, Edo. Bolivar, June 1987, R.C. Dalgleish.

**Remarks.** This is the second of three species for which both sexes have a distinct median gap in the abdominal tergal setal rows. It is easily separated from *M. lightae* by the female having a normal abdominal tergite I and an enlarged tergite II (Fig. 5 vs. Fig. 1). Further differences involve both sexes being consistently smaller than the other two, having typically only three or four setae in each sternite II aster instead of usually five for the other species, and having fewer setae on the abdominal sternites.

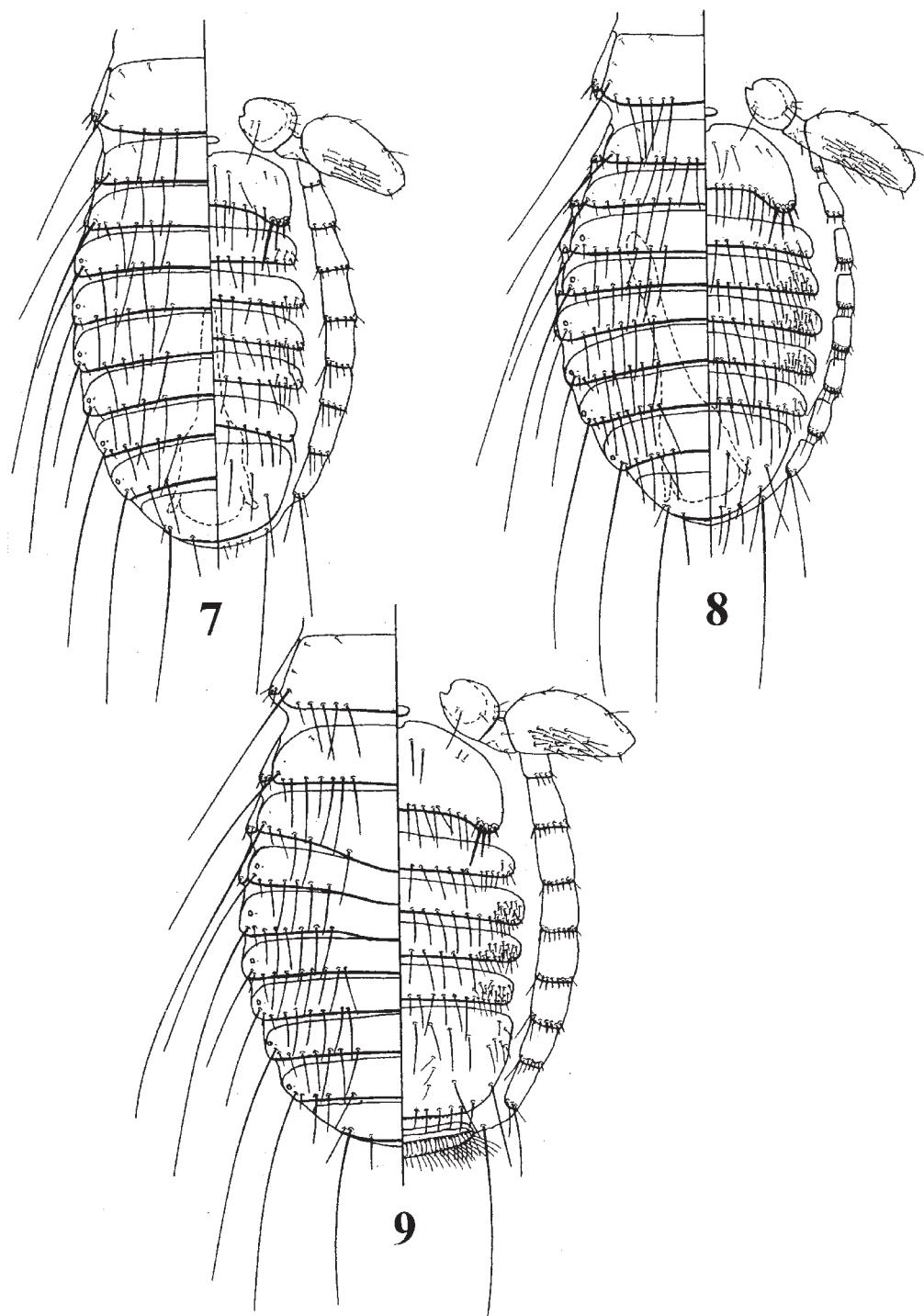
**Etymology.** This species is named in honor of John Klicka, Marjorie Barrick Museum, University of Nevada, Las Vegas, Nevada, in recognition of his assistance in collecting the lice in this study and for his contributions to the systematics of the Cardinalidae.

***Myrsidea markhafneri* Price, Johnson, and Dalgleish, new species**  
(Figs. 8–9)

**Type host.** *Saltator grossus* (Linnaeus, 1766), the Slate-colored Grosbeak.

**Female.** Head with strongly developed hypopharyngeal sclerites; gula usually with 5 setae on each side, less often 6. Dorsoventral metathorax and abdomen as in Fig. 9. Metanotal posterior margin with 11–13 setae; metasternal plate with 6–7 setae. Tergite I of normal size, tergite II moderately enlarged with pronounced rounded medioposterior convexity, resulting in slight compression of tergites III–IV. Each tergal setal row with distinct median gap. Tergal setae: I, 15–17; II, 10–12; III, 13–14; IV, 15–16; V, 17–19; VI, 17–20; VII,

18–19; VIII, 9–12. Postspiracular setae on V–VI about 0.20 long, III 0.30 long, and VII extremely long (0.40). Pleurites: I–IV with relatively uniform short setae; V–VII with fine longer setae toward midline; VIII with long seta flanked on each side by much shorter seta. Sternal setae: II, 4 in each aster, 17–19 marginal between asters, 7–9 anterior; III, 28–29; IV, 55–61; V, 59–66; VI, 50–61; VII, 19; VIII–IX, 21–24. Anus with 36 ventral, 37–42 dorsal fringe setae. Dimensions: TW, 0.51–0.54; HL, 0.33–0.34; PW, 0.32–0.34; MW, 0.50–0.54; AWIV, 0.65–0.73; ANW, 0.23–0.26; TL, 1.63–1.68.



**FIGURES 7–9.** 7. *Myrsidea johnklickai*, male dorsoventral metathorax and abdomen. 8–9. *M. markhafneri*. 8. Male dorsoventral metathorax and abdomen. 9. Female dorsoventral metathorax and abdomen.

**Male.** Head, thorax, median gap in abdominal tergal setal rows, lengths of postspiracular setae, and chae-

totaxy of abdominal pleurites as for female (Fig. 8), except for 10–13 marginal metanotal setae, 6 metasternal plate setae, and no median gap in tergal setal row on I. Tergal setae: I, 16–19; II, 12–15; III, 13–15; IV, 15–17; V, 16–20; VI, 16–20; VII, 16–18; VIII, 9–12. Sternal setae: II, 4 in each aster, less often 3, 15–17 marginal between asters, 6–11 anterior; III, 23–27; IV, 41–52; V, 50–55; VI, 44–50; VII, 20–23; VIII, 5–6. Genitalia and genital sac sclerite as for *M. lightae* (Figs. 2, 3). Dimensions: TW, 0.46–0.48; HL, 0.31–0.33; PW, 0.29–0.31; MW, 0.39–0.42; AWIV, 0.51–0.55; GL, 0.42–0.47; TL, 1.38–1.42.

**Type material.** Holotype female (to USNM), ex *S. grossus*, **PERU (Northeast):** Explor Napa Camp, Rio Napa, SE Iquitos, 14 June 1989, RCD et al. Paratypes: (to INHS) 1 female, 1 male, (to USNM) 1 female, 4 males, same data as holotype.

**Remarks.** This is the third and final species treated in this paper for which both sexes have the abdominal tergal setal rows with a pronounced median gap. The female of *M. markhafneri* is recognizable from the others by having tergite I relatively unmodified and a more modest development of tergite II (Fig. 9 vs. Figs. 1, 5). The consistently larger dimensions and very large number of abdominal sternal setae will further separate both sexes of this species from those of *M. johnklickai*. The large dimensions and certain other features more resemble *M. lightae*, but both sexes of *M. markhafneri* have only four, less often three, setae in each sternite II aster, have fewer setae on the metanotal margin and each of tergites II–IV, and more setae on sternites V and VI.

**Etymology.** This species is named in honor of Mark Hafner, Louisiana State University, Baton Rouge, Louisiana, in recognition of his work on louse systematics and coevolution.

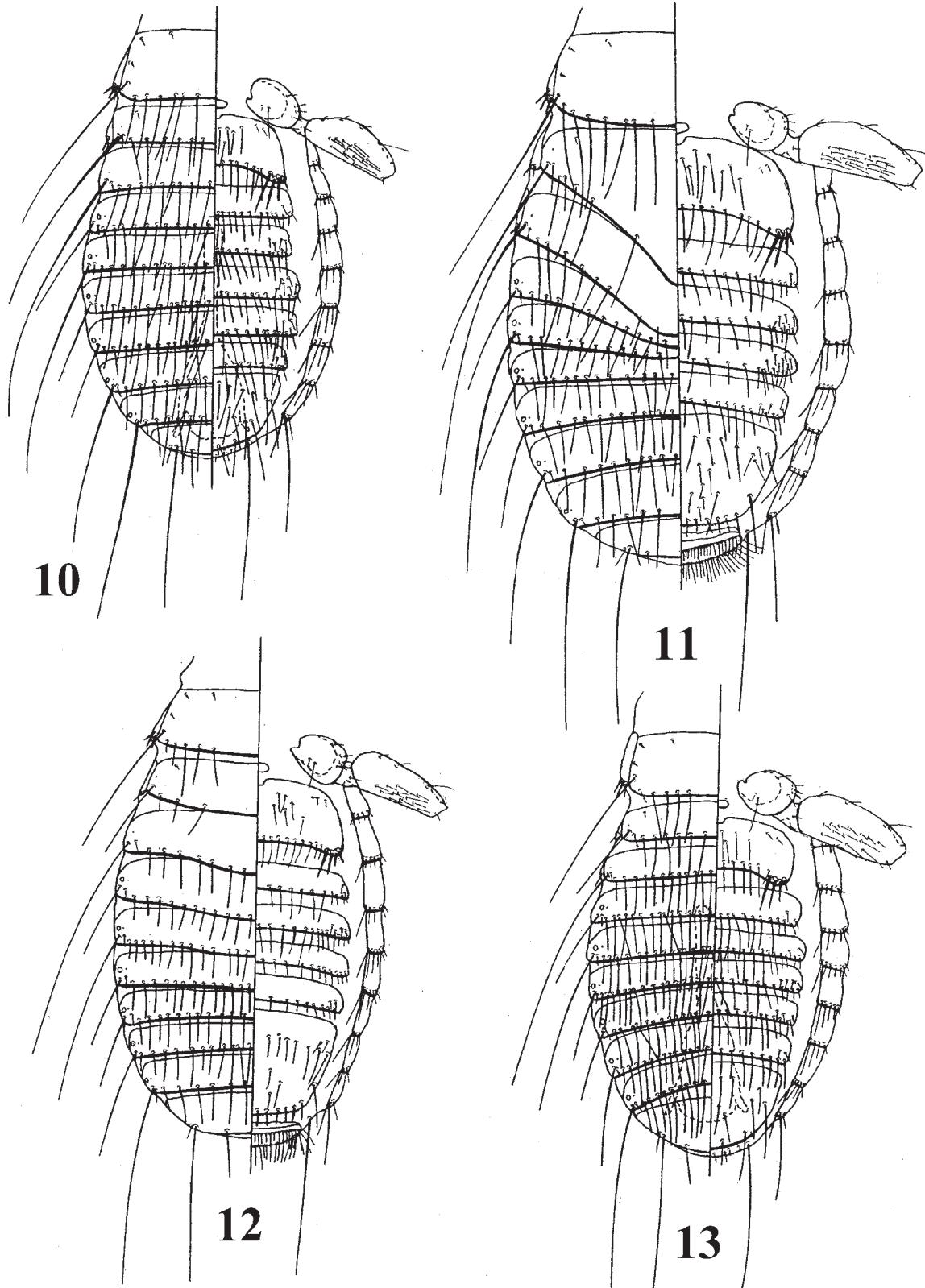
***Myrsidea sychrai* Price, Johnson, and Dagleish, new species**  
(Figs. 10–11)

**Type host.** *Cyanocompsa cyanoides* (Lafresnaye, 1847), the Blue-black Grosbeak.

**Female.** Head with strongly developed hypopharyngeal sclerites; gula with 5 setae on each side. Dors-oventral metathorax and abdomen as in Fig. 11. Metanotal posterior margin with 16–17 setae; metasternal plate with 8–9 setae. Tergite I much enlarged with pronounced tapered medioposterior convexity, this resulting in distortion of tergites II–V. Tergal setae, except on I, with continuous row across segment. Tergal setae: I, 12–15; II, 18–21; III, 24–26; IV, 25–32; V, 25–32; VI, 26–30; VII, 20–26; VIII, 14–16. Postspiracular setae on III, V, and VI not >0.20 long, and VII extremely long (>0.35). Pleurites: I–II with relatively uniform short setae; III–VII with fine longer setae toward midline; VIII with long seta flanked on each side by much shorter seta. Sternal setae: II, 4 in each aster, less often 5, 18–22 marginal between asters, 15–22 anterior; III, 26–33; IV, 39–42; V, 42–47; VI, 34–37; VII, 15–19; VIII–IX, 26–30. Anus with 34–44 ventral, 36–38 dorsal fringe setae. Dimensions: TW, 0.55–0.56; HL, 0.31–0.35; PW, 0.33–0.34; MW, 0.51–0.55; AWIV, 0.65–0.71; ANW, 0.26–0.27; TL, 1.54–1.63.

**Male.** Head, thorax, absence of median gap in abdominal tergal setal rows, lengths of postspiracular setae, and chaetotaxy of abdominal pleurites as for female (Fig. 10), except for 13 marginal metanotal setae, 8 metasternal plate setae, and continuous tergal setal row on I. Tergal setae: I, 17; II, 23; III–IV, 25; V, 28; VI, 24; VII, 21; VIII, 14. Sternal setae: II, 4 in each aster, 16 marginal between asters, 15 anterior; III, 27; IV, 37; V, 39; VI, 35; VII, 21; VIII, 12. Genital sac sclerite distorted but perhaps close to *M. johnklickai* (Fig. 6). Dimensions: TW, 0.48; HL, 0.31; PW, 0.31; MW, 0.41; AWIV, 0.53; GL, 0.42; TL, 1.36.

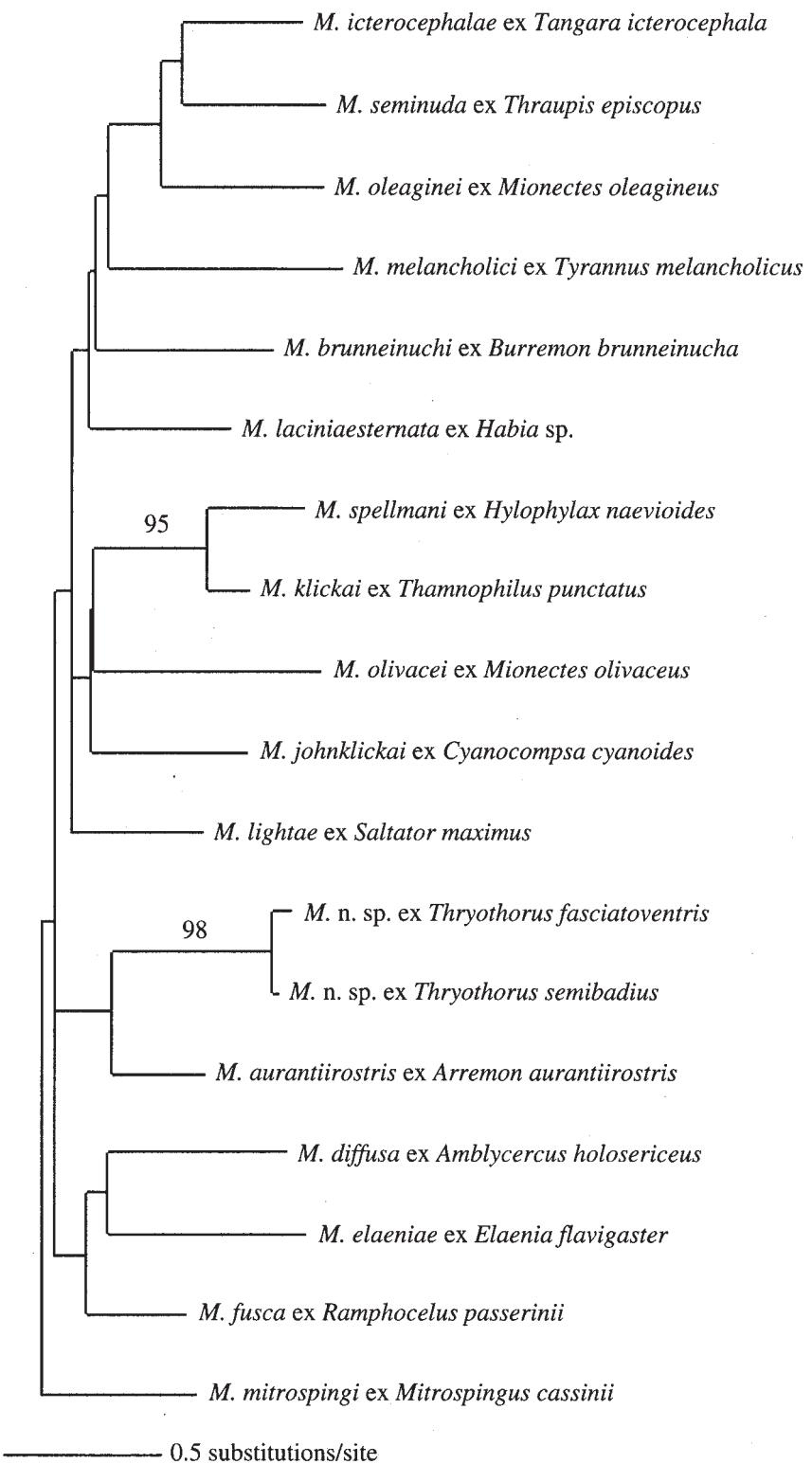
**Type material.** Holotype female (to USNM), ex *C. cyanoides*, **COSTA RICA:** Wilson Botanical Garden, Las Cruces, Cota Brus, Puntarenas, 11 June 1992, Fisher. Paratypes: (to INHS) 1 female, (to USNM) 2 females, 1 male, same data as holotype.



**FIGURES 10–13.** 10–11. *Myrsidea sychrai*. 10. Male dorsoventral metathorax and abdomen. 11. Female dorsoventral metathorax and abdomen. 12–13. *M. pittendrighi*. 12. Female dorsoventral metathorax and abdomen. 13. Male dorsoventral metathorax and abdomen.

**Remarks.** This is the first of two species that differ from the previous three by having the majority to all of the abdominal tergal setae in a complete row across the segment, without a median gap. Both sexes of *M.*

*sychrai* differ from the following species by being larger in all dimensions, by having more metasternal setae and more setae on tergites III–VI, and by having longer postspiracular setae on VII. The female is conspicuously different by having a much enlarged tergite I and different sizes of tergites II–V (Fig. 11 vs Fig. 12). The male has more anterior setae on sternite II and more total setae on sternites III–VI.



**FIGURE 14.** Phylogeny of various *Myrsidea* species derived from maximum likelihood analyses of 379 bp of the mitochondrial COI gene. Searches involved 10 random addition replicates using a GTR + I + G model. Numbers above branches are support from 100 likelihood bootstrap replicates. Branches are proportional to substitutions per site (scale indicated). Tree rooted on *Dennyus hirundinis* (Linnaeus, 1761) (not shown). *M.* = *Myrsidea*.

This is the second new species of *Myrsidea* to be described from *C. cyanoides* in this paper. The type series was collected only in Costa Rica at a site similar to that where a series of *M. johnklickai* was collected. However, the hosts for these two new species had only a single species on each and we have confidence in the uniqueness of these species.

**Etymology.** This species is named in honor of Oldrich Sychra, University of Veterinary and Pharmaceutical Science, Brno, Czech Republic, in recognition of his work on the taxonomy of Neotropical lice.

***Myrsidea pittendrighi* Price, Johnson, and Dalglish, new species**  
(Figs. 12–13)

**Type host.** *Saltator striatipectus* Lafresnaye, 1847, the Streaked Saltator.

**Female.** Head with strongly developed hypopharyngeal sclerites; gula with 5, less often 4, setae on each side. Dorsoventral metathorax and abdomen as in Fig. 12. Metanotal posterior margin with 11–12 setae; metasternal plate with 6 setae. Tergites I–III only slightly enlarged with II–IV having very small medioposterior convexity. Tergal setae, except on I, with continuous row across segment. Tergal setae: I, 8; II, 18–23; III, 26–31; IV, 31–33; V, 30; VI, 26–27; VII, 25–26; VIII, 17–19. Postspiracular setae on I, III, V, and VI not >0.20 long, and on VII 0.25 long, much shorter than extremely long setae on VIII. Pleurites: I with relatively uniform short setae; II–VII with fine longer setae toward midline; VIII with long seta flanked on each side by much shorter seta. Sternal setae: II, 4 in each aster, 15–16 marginal between asters, 14–15 anterior; III, 23–26; IV, 32–33; V, 34–35; VI, 27–29; VII, 17; VIII–IX, 19. Anus with 30–34 ventral, 31–34 dorsal fringe setae. Dimensions: TW, 0.43–0.45; HL, 0.30–0.31; PW, 0.29; MW, 0.43; AWIV, 0.53–0.56; ANW, 0.20–0.21; TL, 1.46–1.48.

**Male.** Head, thorax, absence of median gap in abdominal tergal setal rows, lengths of postspiracular setae, and chaetotaxy of abdominal pleurites as for female (Fig. 13), except for 12 marginal metanotal setae and continuous row of tergal setae on I. Tergal setae: I, 17; II, 29; III–IV, 32–33; V, 37; VI, 30; VII, 27; VIII, 23. Sternal setae: II, 4 in each aster, 15 marginal between asters, 12 anterior; III, 25; IV, 27; V, 31; VI, 28; VII, 21; VIII, 9. Genital sac sclerite as for *M. lightae* (Fig. 3). Dimensions: TW, 0.39; HL, 0.28; PW, 0.27; MW, 0.35; AWIV, 0.45; GL, 0.40; TL, 1.22.

**Type material.** Holotype female (to INHS), ex *S. striatipectus*, **PANAMA:** Serriana del Maje, 16 Feb. 2006, JMD 690, K.P. Johnson. Paratypes (to INHS): 1 female, 1 male, same data as holotype.

**Remarks.** This is the second species described here that has both sexes with a complete row of tergal setae across the majority to all abdominal segments. It differs from *M. sychrai* that also shows this feature by the female with much smaller anterior tergites (Fig. 11 vs. Fig. 12), and by both sexes with much smaller dimensions, with fewer setae on the metasternal plate and tergites III–VI, and with a much shorter postspiracular seta on VII. The male is further separable by having fewer anterior setae on sternite II and fewer total setae on sternites III–VI.

The type series of *M. pittendrighi* is unusual in that it was taken from the same individual host bird that also yielded three specimens of *M. lightae*. We consider it a rarity to find two different species of *Myrsidea* on the same individual, but we opt for recognizing this as a valid record without evidence to the contrary.

**Etymology.** This species is named in honor of Barry Pittendrigh, Purdue University, West Lafayette, Indiana, in recognition of his efforts to organize and obtain the first complete sequences of a louse genome, which will be a great asset to work on the systematics of lice.

## Discussion

The passerine family Cardinalidae contains a relatively small number of genera and species, with Dickinson (2003) assigning 11 genera with 41 species to this family. Recent collecting efforts from these hosts by KPJ

and RCD succeeded in collecting *Myrsidea* from two genera and four species. A study of these has revealed that they represent five new species of *Myrsidea*.

Highly distinctive morphological differences exist among these five species, again confirming the high degree of host specificity exhibited by the *Myrsidea* in general. While earlier studies of *Myrsidea* generally have supported the concept of one louse species per host taxon, *M. lightae* occurs on two host species across multiple localities, making this louse species not completely host specific. In addition we found two cases of the same species of bird hosting two species of *Myrsidea* in one case on the same individual bird and the other on two different birds. Considering the profound differences among the five *Myrsidea* new species described in this paper, it would seem most likely that there are many more new louse species awaiting further collecting from this host family.

Sequences of a 379 base pair portion of the mitochondrial COI gene (GenBank accession numbers EU289211-EU289212) were obtained for *Myrsidea lightae* from *Saltator striatipectus* and *M. johnklickai* from *Cyanocompsa cyanoides*. These lice were collected at the same locality in Panama. Uncorrected percent sequence divergence between these two species was 21.6%. In comparison with several other New World species of *Myrsidea* (Fig. 14), all other species differed from these two by at least 17% uncorrected sequence divergence. These divergences exceed those between many other described species (Price and Johnson 2006a, 2006b; Johnson and Price 2006) and support the distinctiveness of these two species. Maximum likelihood analyses of these COI sequences suggest that the two species of *Myrsidea* sequenced from Cardinalidae are not each other's closest relatives, though many aspects of the phylogeny from these data are not strongly supported by bootstrapping (Fig. 14).

## Acknowledgments

Collecting in Costa Rica by RCD was aided by Robert L. Fisher, Juniata College, Huntingdon, Pennsylvania. We also are grateful to Jeff DaCosta, Peggy Guttan-Mayerma, John Klicka, Matthew Miller, and Garth Spellman for their assistance to KPJ in collecting in Panama. This work was supported in part by NSF grants PEET DEB-0118794 and DEB-0612938 to KPJ.

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